

OSTEOLOGY AND MYOLOGY OF THE HEAD AND NECK REGIONS OF *CALLISAURUS*, *COPHOSAURUS*, *HOLBROOKIA*, AND *UMA* (REPTILIA: IGUANIDAE)

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ABSTRACT.—A detailed study of the anterior osteology and myology of *Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma* reveals the phylogenetic relationships among the sand lizards. An SPSS discriminant analysis of osteological characters combined with myological characters indicates that *Callisaurus* is most primitive, *Cophosaurus* and *Holbrookia* are most closely related, and *Uma* is the most distinct of the sand lizard genera. Because of close relationships between *Cophosaurus* and *Holbrookia*, it is postulated that earlessness evolved once, and *Cophosaurus* is returned to synonymy under *Holbrookia*.

Blainville (1835) wrote the first description of a sand lizard and named it *Callisaurus draconoides*. Since then various authors have published articles concerning sand lizards. Girard (1851) described *Holbrookia maculata*, Trochel (1852) described *Cophosaurus texanus*, and that same year Baird and Girard synonymized *Cophosaurus* with *Holbrookia*, providing the name *Holbrookia texana*, which then remained unchanged for over 100 years. Subsequently, Baird (1858) described *Uma notata*.

By 1858 all genera represented in the sand lizard group had been described. Since then new species and subspecies, as well as new combinations, have been added by various authors as follows: Bocourt (1874) *Holbrookia elegans*; Cope (1880, 1883, 1894, 1895, 1896, 1900) *Holbrookia lacerata*, *Holbrookia maculata flavilenta*, *Uma scoparia*, *Uma inornata*, *Uma rufopuncatata*, *Callisaurus crinitus*, *Callisaurus rhodostictus*, *Holbrookia maculata maculata*, *Callisaurus draconoides ventralis*, and *Callisaurus ventralis gabbii*; Stejneger (1890) *Holbrookia maculata approximans* and *Holbrookia maculata lacerata*; Richardson (1915) *Callisaurus ventralis myurus*; Dikerson (1919) *Callisaurus carmenensis*; Schmidt (1921, 1922) *Holbrookia maculata campi*, *Holbrookia pulchra*, *Holbrookia dickersonae*, and *Callisaurus ventralis inusitatus*; Schmidt and Bogert (1947) *Uma exsul*; Barbour (1921) *Holbrookia thermophila*; Harper

(1932) *Holbrookia propinqua stonei*; Smith (1935, 1943, 1946:137, 145) *Holbrookia elegans thermophila*, *Holbrookia elegans elegans*, *Holbrookia bunkerii*, *Holbrookia maculata ruthveni*, *Holbrookia maculata dickersonae*, *Holbrookia maculata pulchra*, and *Holbrookia maculata thermophila*; Linsdale (1940) *Callisaurus draconoides myurus* and *Callisaurus draconoides gabbii*; Heifetz (1941) *Uma notata notata*; Bogert and Dorsom (1942) *Callisaurus draconoides brevipes*; Smith and Burger (1950) *Holbrookia propinqua propinqua* and *Holbrookia propinqua piperata*; Peters (1951) *Holbrookia texana texana* and *Holbrookia texana scitula*; Axtell (1956) *Holbrookia lacerata*, *Holbrookia lacerata subcaudalis* and *Holbrookia maculata perspicua*; Smith and Cochran (1956) *Callisaurus draconoides rhodostictus*; and Williams, et al. (1959) *Uma paraphygus*.

Some summaries, reviews, checklists, and comparative studies have also been written. Cope (1896) synonymized *Uma* and *Callisaurus* in a short paper discussing the genus *Callisaurus*. He recognized *Uma* again in his large work on the crocodilians, lizards, and snakes of North America (1900) and recognized one species and three subspecies of *Callisaurus*.

Smith (1946:137, 145), in his "Handbook of Lizards," recognized in *Callisaurus* one species and ten subspecies and stated (p. 145): "The whole group of *Callisaurus* of

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western United States is in need of revision. The subspecies are not adequately characterized, nor are their ranges well worked out. There is very little information on the life history." Although we now know much more about the life history of *Callisaurus*, it is still in need of a comprehensive taxonomic review and remains a monotypic genus. (A careful revision for *Callisaurus* has not yet been attempted.)

The genus *Holbrookia* has had two revisions. Schmidt (1922) made the first; a second was by Axtell (1958). Schmidt (p. 709) stated: "The taxonomy of the North American lizards of the genus *Holbrookia* Girard offers one of the most interesting and difficult problems in North American herpetology."

He recognized several species and states that (p. 712) "*Holbrookia* is obviously directly related to *Callisaurus*, from which it differs only in the concealed tympanum and with which it agrees in general features of color pattern and scutellation."

Smith (1946:137, 145) doubts that a practical means of characterizing the species exists and believes that "until such a means is found there will remain indefinitely a problem in defining the ranges of the several subspecies, or in defending their actual validity. Accordingly the genus, particularly the *maculata* group, merits a careful study perhaps more than any other in the United States."

Axtell (1958) recognized only three species, *Holbrookia lacerata*, *H. propinqua*, and *H. maculata*. He considered *H. texana* to be a species of the genus *Callisaurus* and therefore did not discuss it. He did list two subspecies for *lacerata*, two for *propinqua*, and 11 for *maculata*.

Uma has been reviewed by Heifetz (1941), Norris (1958), and Mayhew (1964b). Heifetz recognized *U. notata notata*, *U. notata cowlesi*, *U. inornata*, and *U. scoparia*. He also referred to the taxonomic confusion that exists because of erroneous type localities in this genus. In his checklist Schmidt (1953) recognized only one species (*notata*), with three subspecies (*notata*, *inornata*, and *scoparia*).

Norris (1958) recognized *Uma n. notata*,

U. n. rufopunctata, *U. n. inornata*, *U. scoparia*, and *U. exsul*. He discussed the evolution of *Uma* and its relationship to other sand lizards.

The conflict relative to the classification of the *notata-scoparia* group was discussed by Mayhew (1964b). He recognized *U. inornata*, *U. notata*, and *U. scoparia* all as full species on the basis of temperature tolerance and reproductive data.

Peters (1951) reviewed *Holbrookia texana* (*Cophosaurus texanus*). He described two subspecies, but mentions little concerning relationships with other sand lizards.

Clarke (1965) revived *Cophosaurus texanus* on the basis of behavioral data collected in a large comparative study of the sand lizard group.

Ecological and behavioral studies concerning sand lizards have also been published by Burt (1931a, 1931b), Stebbins (1944, 1954, 1966), Ramsey (1948, 1949), Cagle (1950), Williams and Smith (1958), Axtell (1960), Lannom (1962), Carpenter (1963, 1967), Clarke (1965), Mayhew (1964a, 1964b, 1966), Pianka and Parker (1972), Tanner and Krogh (1975), and Judd (1974, 1975).

The anatomy of these lizards has not been thoroughly studied. Earle, in a series of articles (1961a, 1961b, 1961c, 1962), described in detail the comparative anatomy of the middle ear of sand lizards. Stebbins (1943, 1944) described the nasal structures and some aspects of the ecology of *Uma*, then (1948) described the nasal structures of lizards in general, which included the sand lizards. Axtell (1958) described the osteology of *Holbrookia* and stated that it is essentially the same as found in all sand lizards. Etheridge (1964) studied the skeletal morphology of sceloporine lizards, which includes sand lizards, and compared their relationships. Savage (1958) studied *Urosaurus* and *Uta* and made remarks concerning related genera, which included sand lizards. A few references to sand lizards were made by Larsen and Tanner (1974) while studying *Sceloporus*, and Guttman (1970b) also refers to them in his electrophoretic study of the hemoglobins of sand lizards. He found that

all genera possessed the same major and minor protein components.

Only portions of the osteology have been adequately treated; the myology is essentially untouched. The objectives of this study are to: (1) describe the skull osteology and branchiomic myology of sand lizards; (2) identify osteological and myological characteristics that distinguish the sand lizard generic groups; and (3) determine more accurately the relationships between these groups. No attempt will be made to deal with the species and subspecies except as they relate to the generic phylogeny.

MATERIALS AND METHODS

Specimens used were obtained from the Brigham Young University Life Sciences Museum (BYU), the California Academy of Sciences (CAS), and the Strecker Museum at Baylor University. At least four specimens from each of the four genera were used for osteological examinations. The myology of these 16 specimens, plus four additional individuals from each genus, were also used in developing the myological description. The following list indicates the material used: *Callisaurus draconoides gabbi* from N.T.S., Nye Co., Nevada: (BYU) 2943, 2967, 3079, 40037; *C. d. inusatus* from Tiburon Island, Sonora, Mexico: (BYU) 30175, 30176, 30178; *C. d. splendidus* from Isla Angel de la Guardia, Gulf of California, Mexico: (BYU) 41112; *C. d. carmenesis* from Baja California Sur, Mexico: (BYU) 41095, 41231; *Cophosaurus texanus texanus* from Chihuahua, Mexico: (BYU) 14339, 15712; *C. t. scitula* from Sierra Co., New Mexico: (BYU) 30512, 30513, 30515; *C. t. scitula* from Pima Co., Arizona: (BYU) 34331, 34336; *Holbrookia lacerata* from Giaraz Co., Texas: (CAS) 73979; *H. maculata approximans* from Colonia Dublan, Mexico: (BYU) 11370, 17099; *H. maculata bunkeri* from Chihuahua, Mexico: (BYU) 15782, 15785, 15788, 15789; *H. propinqua propinqua* from Padre Island, Cameron Co., Texas: (CAS) 16187; *Uma notata inornata* from Riverside Co., California: (BYU) 3263, 3266, (CAS) 22824, 22826; *U. n. cowlesi* from Sonora, Mexico: (BYU) 30144, 30156; *U. scoparia*

from San Bernardino Co., California: (BYU) 11389, (CAS) 42072.

Skeletal material was prepared by careful dissection. Bones were cleaned with forceps and dissecting needles and soaked in Clorox bleach for several minutes to loosen soft tissues, after which further picking and cleaning was done. Skulls were not allowed to dry, but were preserved in 70 percent EtOH to insure that cartilaginous skeletal elements could be examined.

The Statistical Package for the Social Sciences (SPSS) discriminant analysis was utilized to aid in the identification of characters where they were not already obvious. The statistical analysis will be described below.

Myological examinations consisted of careful dissection in which each muscle was separated and its origin and insertion determined. General morphology (shape, relative size, and position) of each muscle was also noted. Muscle comparisons are based on both origin-insertion and muscle morphology. Only the branchiomic muscles associated with the hyoid arch and the jaws are described.

OSTEOLOGY

Sand lizard skulls have been examined in detail. The length and width of individual elements were measured with a Golgau vernier caliper and a five-millimeter mini-tool. Comparisons were made on the basis of ratios, as well as on the shape and position of each bone in relation to other articulating bones. The lower jaw and hyoid have been studied in the same manner.

The skull is streptostylic, with a freely movable quadrate bone. In mature individuals the ethmoid region of the braincase proper is not ossified, but consists of cartilage plates from which cartilaginous rods extend dorsad to add to and support the membranes that protect the brain. Eyes are large, and only a thin sheet of cartilage separates them medially; there is no apparent area of ossification, even in mature individuals.

The sand lizard skull follows the basic plan of Sceloporine lizards as described by

Ethridge (1964) and Larsen and Tanner (1974, 1975); there is a great deal of uniformity within the sand lizard group. We will not give detailed descriptions of each bone here; however, these data are available to those who may desire them. We will, however, describe the variations from the Sceloporine skull as well as the differences between the sand lizard genera.

The following is a list of the skeletal elements measured and described (they are illustrated on Figs. 1, 2, 3, 4):

Basioccipital	Jugal
Supraoccipital	Postorbital
Vomer	Dentary
Maxilla	Splénial
Frontal	Hyoid
Parietal wing	Posttemporal fossa
Quadrate	Exoccipital
Surangular	Ectopterygoid
Coronoid	Premaxilla
Orbit	Prefrontal
Supratemporal fossa	Parietal
Basisphenoid	Squamosal
Pterygoid	Articular
Palatine	Angular
Nasal	Temporal fossa
Infraorbital fossa	

The sand lizard skulls differ from the general sceloporine skull in that they lack the lacrimal and the postfrontal bones. They differ among themselves in several ways, but most of the variance seems to be associated with the posterolateral position of the skull. The discriminant analysis selected 116 ratios that could aid in discriminating the four genera. Six measurements were found to be important. Every ratio selected included at least one of these six. They are listed along with their frequency of use: squamosal width (26), quadrate length (26), mandible length (20), hyoid length (20), mandible width (19), and maxillary length (15).

Representative ratio comparisons are given to illustrate the separation and relationships of genera. Figures (1-4) of the lateral, dorsal, and ventral aspects of the skull are also presented, including the lateral and medial views of the lower jaw and the dorsal view of the hyoid.

Earl (1961a, 1961b, 1961c, and 1962) reported on the osteological variations in the ear and indicated that all four genera were

distinct, with *Cophosaurus* midway between *Callisaurus* and *Holbrookia*.

One of the first variations noticed, as skulls were being prepared, was that *Cophosaurus* and *Holbrookia* had a para-occipital process directed anterolaterally. That of *Callisaurus* and *Uma* is directed lateral or slightly posterior. As a result of this variation, variations in the length and width of the quadrate, squamosal, jugal, and postorbital were noted. In *Uma* and *Callisaurus* the ventral articulating process is ventral to the basioccipital, whereas in *Cophosaurus* and *Holbrookia* the quadrate is much shorter. *Uma* and *Callisaurus* also have a wider squamosal, and the squamosal and jugal just meet. In the earless genera the jugal pushes in between the squamosal and postorbital. In one *Uma* individual the squamosal and jugal failed to meet, and the postorbital had pushed in between them. Some other variations (such as the configuration of sutures between the frontal and parietal, the frontal and nasals, the basisphenoid and basioccipital, and the maxilla and premaxilla, as well as proportional variations in the maxilla, postorbital, and premaxilla) were also found, but they were slight and had no significance. These are attributed to individual variation on the species or subspecies level.

MYOLOGY

The myology of the neck and throat region has been carefully studied. Axtell (1958) pointed out that the intermandibularis muscle in the most anterior region of the throat is degenerate. The genioglossus is therefore the most ventral muscle in that region. This condition is constant throughout the sand lizard genera. The variations within the sand lizard genera are found in the intermandibularis muscles, depressor mandibularis, constrictor colli, and the omohyoideus-sternohyoideus complex.

The *intermandibularis anterior superficialis* (Figs. 5, 6) is a small muscle. In *Uma*, it is distinctly fan shaped. In *Callisaurus* and *Holbrookia* it is not fan shaped, and *Cophosaurus* shows a slight amount of fanning. In *Holbrookia* the fibers of this

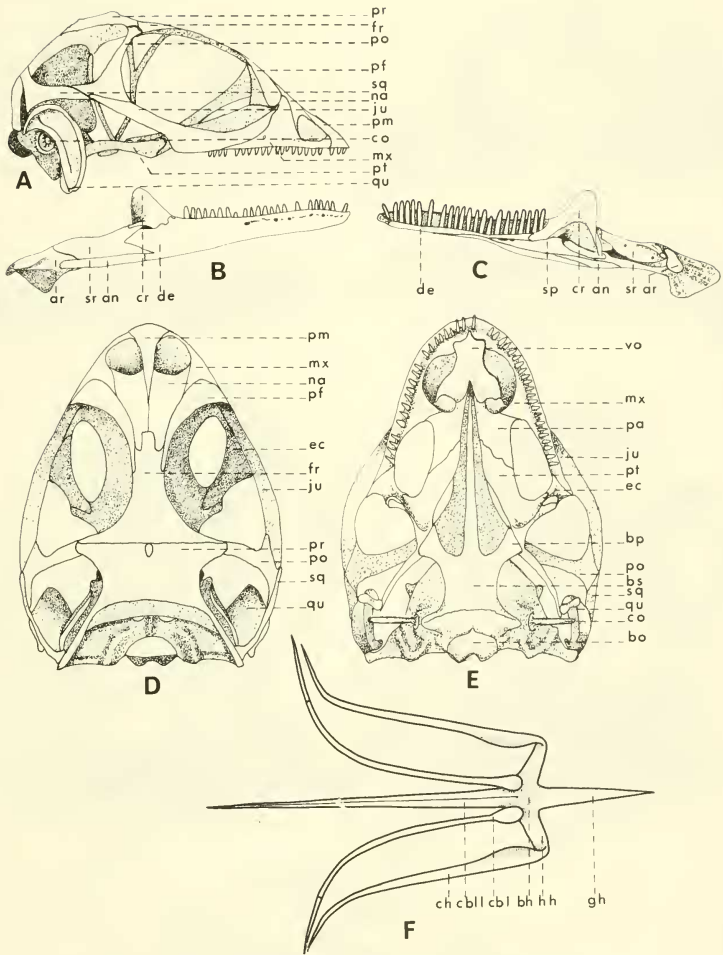


Fig. 1. The skull osteology of *Callisaurus* BYU 3079: A. lateral view of skull; B. lateral view of lower jaw; C. medial view of lower jaw; D. dorsal view of skull; E. ventral view of skull; F. dorsal view of hyoid. The symbols used are:

- | | | | |
|-------------------------|------------------|-----------------|---------------|
| an-angular | ch-ceratohyal | ju-jugal | pr-parietal |
| ar-articular | co-columella | mx-maxilla | pt-ptyergoid |
| bh-basihyal | cr-coronoid | na-nasal | qu-quadrates |
| bo-basioccipital | de-dentary | pa-palatine | sq-squamosal |
| bp-basiptyergoid | ec-ectopterygoid | pf-prefrontal | sr-surangular |
| bs-basisphenoid | fr-frontal | pm-premaxilla | vo-vomer |
| cbI-ceratobranchial I | gh-glossohyal | po-post orbital | |
| cbII-ceratobranchial II | hh-hypohyal | | |

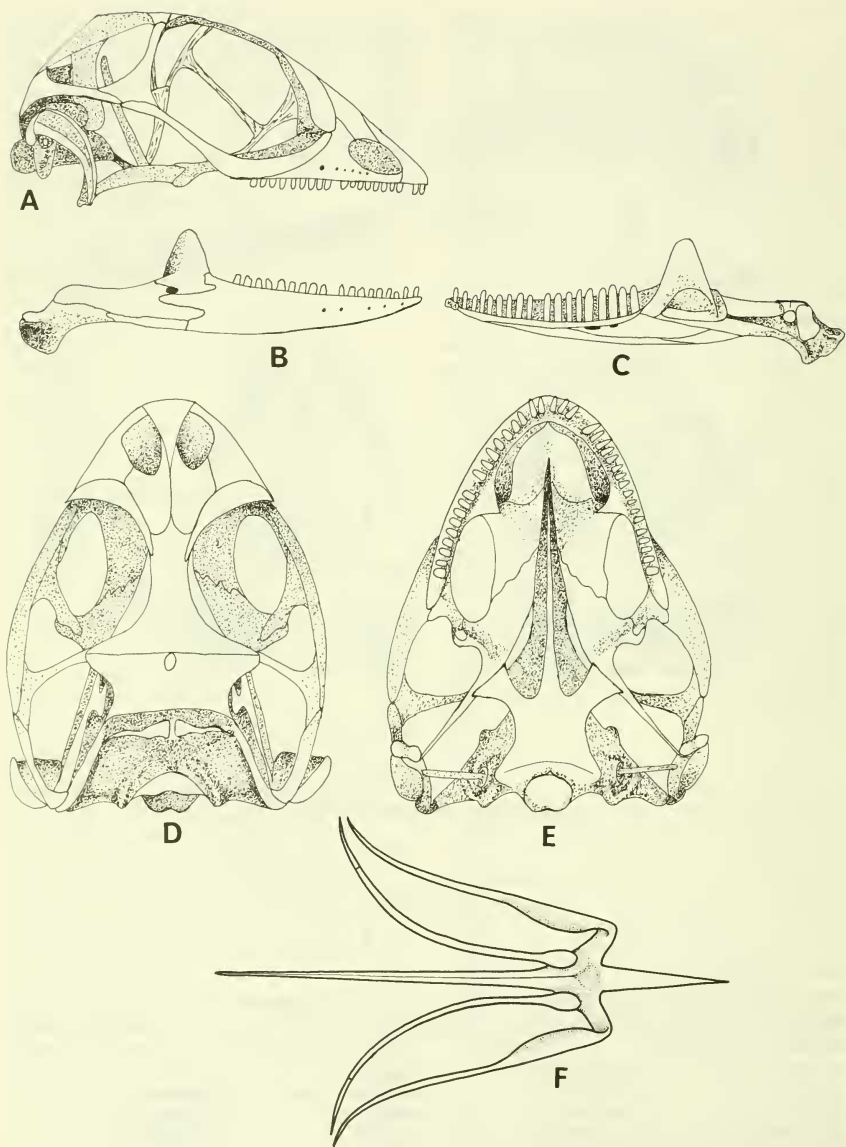


Fig. 2. The skull osteology of *Uma* BYU 3266: A; B; C; D; E; F; same as Fig. 1. The symbols used are the same as Fig. 1.

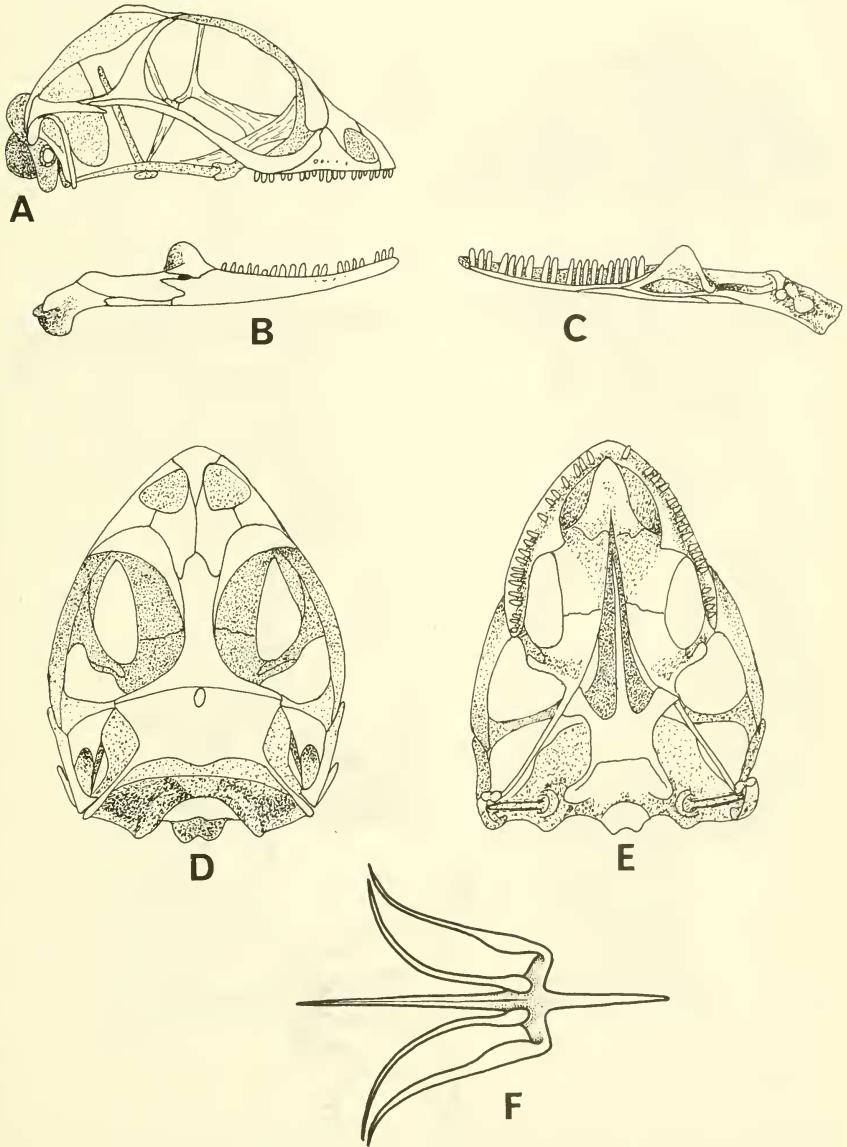


Fig. 3. The skull osteology of *Holbrookia* BYU 15783: A; B; C; D; E; F; same as Fig. 1. The symbols used are the same as Fig. 1.

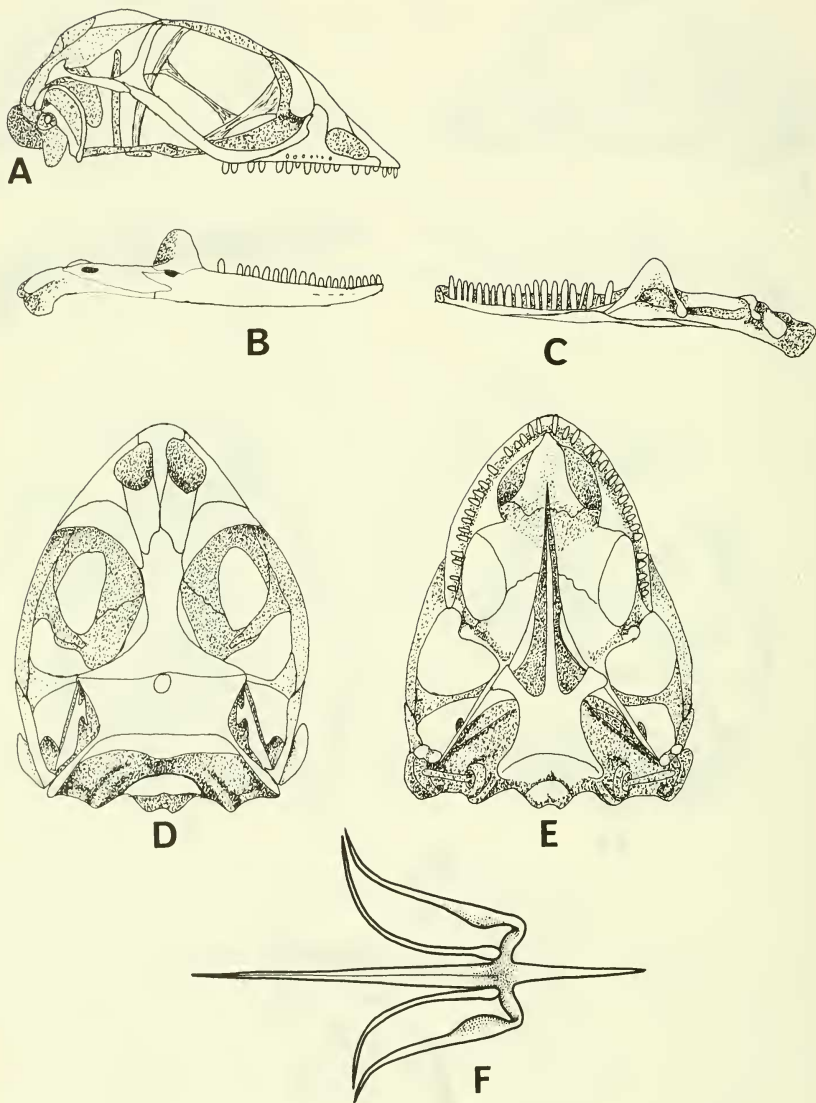


Fig. 4. The skull osteology of *Cophosaurus* BYU 30518: A; B; C; D; E; F; same as Fig. 1. The symbols used are the same as Fig. 1.

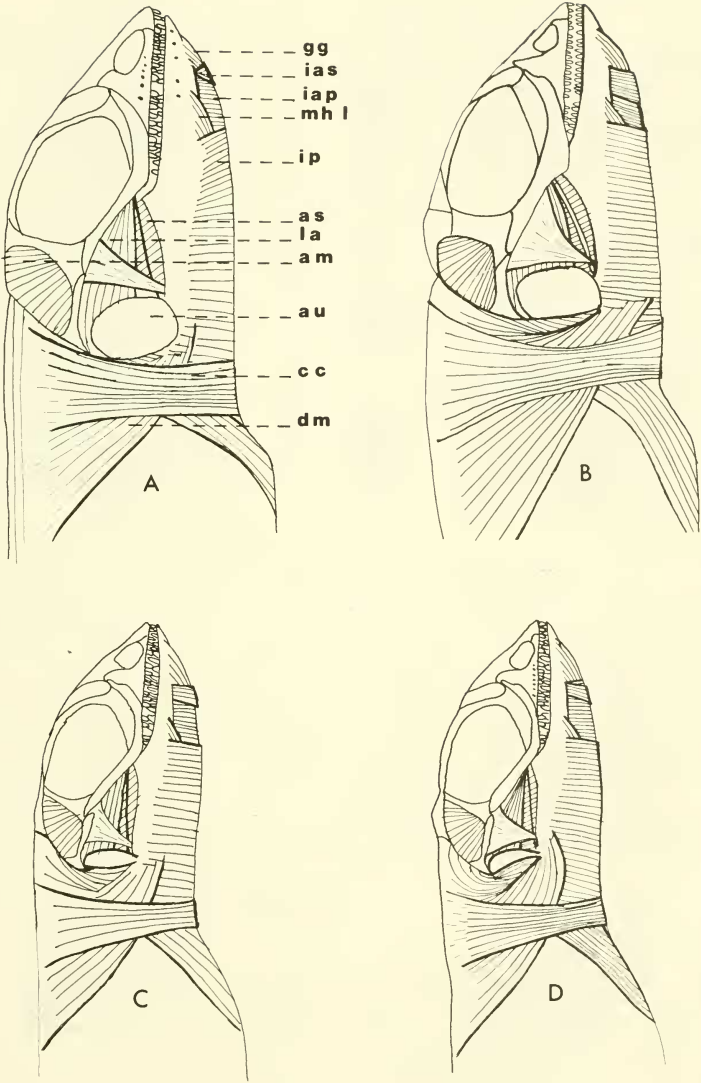


Fig. 5. Lateral view of head and neck musculature; superficial depth. A. *Uma* BYU 3263; B. *Callisaurus* BYU 2943; C. *Holbrookia* BYU 15782; D. *Cophosaurus* BYU 30512. The symbols used are: am-adductor mandibularis externus medius; as-adductor mandibularis externus superficialis; au-auditory meatus; cc-constrictor colli; dm-depressor mandibularis; gg-genioglossus; iap-intermandibularis anterior profundus; ias-intermandibularis anterior superficialis; ip-intermandibularis posterior; la-levator angularis oris; mhl-mandibulohyoideus I.

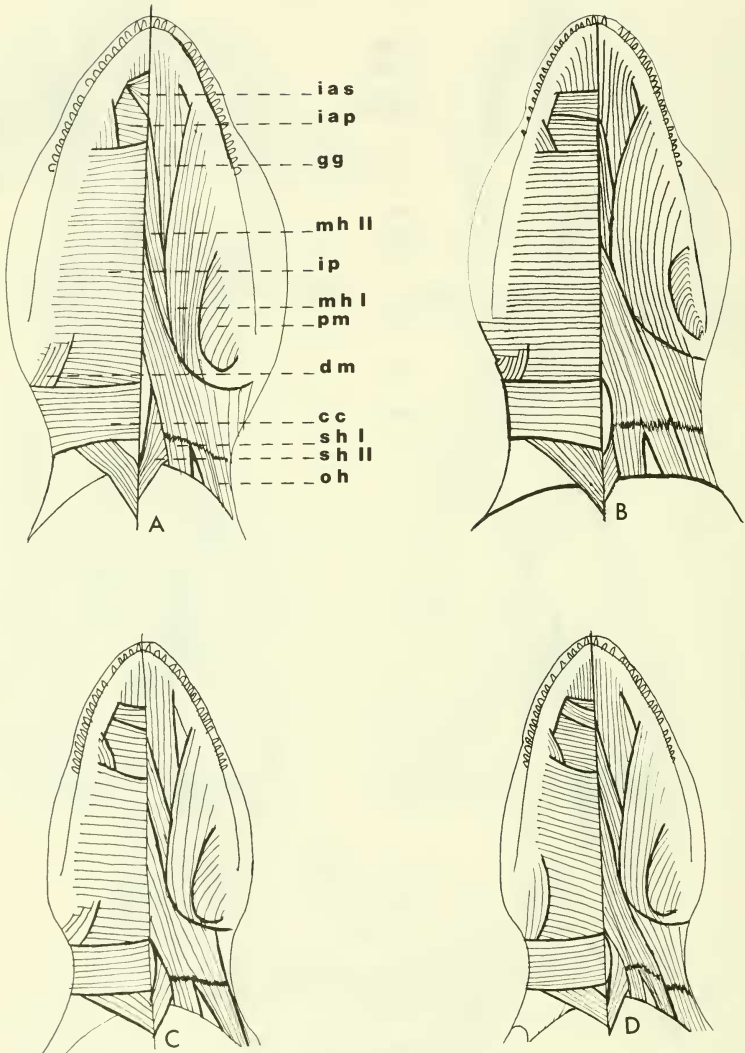


Fig. 6. Ventral view of throat musculature; superficial layer at left and first depth at right. A. *Uma* BYU 3263; B. *Callisaurus* BYU 2943; C. *Holbrookia* BYU 15782; D. *Cophosaurus* BYU 30512. The symbols used are: cc-constrictor colli; dm-depressor mandibularis; gg-genioglossus; iap-intermandibularis anterior profundus; ias-intermandibularis anterior superficialis; ip-intermandibularis posterior; mhI-mandibulohyoideus I; mhII-mandibulohyoideus II; oh-omohyoideus; pm-pterygomandibularis; shI-sternohyoideus I; shII-sternohyoideus II.

muscle pass posteromedial, whereas in the other three genera they pass transversely or fan out.

The *intermandibularis anterior profundus* (Figs. 5, 6) occupies a position posterior and dorsal to the *intermandibularis anterior superficialis*, and anterior and dorsal to the *intermandibularis posterior*. In *Uma* the fibers extend medially, with only a few fibers at each end fanning out. In *Cophosaurus* it is distinctly fan shaped, and in *Callisaurus* it fans out to a lesser degree. In *Holbrookia* it is slightly fan shaped, with most fibers slanting posteriorly. There were two areas of variation seen in the neck musculature.

The *constrictor colli* (Figs. 5, 6) is the superficial muscle of the neck, originating in the dorsolateral fascia of the neck and inserting in the ventral raphe of the throat posterior to the *intermandibularis posterior*. It is one or two muscle fibers thick, rather narrow, and the origin is broader than the insertion.

In all four genera the muscle fibers of the *constrictor colli* reach the mid-throat area, but they originate in a fascia without reaching the dorsal skeletogenous septum.

The *constrictor colli* is widest in *Uma*. It covers from the posterior edge of the tympanum to the shoulder, nearly covering the *depressor mandibularis* completely. In the other three genera it is more straplike and only fills half the space between the posterior edge of the tympanum and shoulder, being centered in this area.

The *depressor mandibularis* (Figs. 5, 6) originates in the mid-dorsal raphe, along the posterior borders of the parietal bone and parietal wings. The insertion has three slips; one inserts deep to the *pterygomandibularis* on the articular process of the lower jaw. Another passes superficially to the *pterygomandibularis* and the *intermandibularis posterior*; it inserts on the ventrolateral surface of the mandibular rami by interdigitating at right angles with these muscles. The third slip inserts on both sides of a tendon that extends dorsally from the articular process. The attachment of this slip to the articular is superficial to the deep slip mentioned above. In the earless lizards (*Cophosaurus* and *Holbrookia*) a portion of this muscle is

expanded anteriorly to partially cover the tympanic cavity.

The *sternohyoideus* I and *omohyoideus* are closely related, and there is considerable confusion in the literature concerning them. The position taken here is that those portions that originate on the scapula and clavicle are *omohyoideus*, and those portions that originate on the sternum are *sternohyoideus*.

Both muscles are deep to the *constrictor colli*, and the *episterno-cleidomastoideus*. The muscle dorsal to them is the *sternohyoideus* II.

The *omohyoideus* (Fig. 6) takes two forms; in *Uma* and most species of *Holbrookia* it has a single head originating on the scapula and clavicle. In *Callisaurus*, *Cophosaurus*, and some *Holbrookia* the *omohyoideus* is divided for its entire length, connected only by a myocomma located midway between the origin and insertion, bisecting the muscle and binding the muscle fibers together. This myocomma also bisects the *sternohyoideus* I, and the two muscles are bound firmly together by it.

The *omohyoideus* can be easily separated from the *sternohyoideus* posterior to the myocomma, but they cannot be distinguished anterior to it except by position.

The *sternohyoideus* I (Fig. 6) originates on the sternum and inserts on the proximal end of the ceratobranchial I and II. The myocomma is at its junction with the *omohyoideus*, and it unites the two muscles. The medial portion of the *omohyoideus* cannot be distinguished from the *sternohyoideus* anterior to this myocomma in all genera.

STATISTICAL ANALYSIS

The osteology of the skulls was analyzed by taking 43 measurements from each skull and by calculating all possible ratios. The Statistical Package for the Social Sciences (SPSS) discriminant analysis was employed to determine which ratios were of value in distinguishing genera and if the lizards could be classified by using them. The theory and use of discriminant analysis is described by Klecka (1975). From each skull 903 ratios were generated, and those suf-

ficient to separate one genus from the other three were used.

The discriminant analysis proceeds in a stepwise fashion by selecting the single best-discriminating variable, and then selects a second on the basis of its ability to improve the value of the discrimination criterion in combination with the first variable. Third and subsequent variables are similarly selected according to their ability to contribute to further discrimination. A plot of the discriminant score in two dimensions, a territorial map, and a classification based on the preceding analysis are given. Range, mean, and standard deviation of ratios for each genus are also given, and examples are presented in Figs. 7 and 8 along with a plot of the ratios (Figs. 7-11) that illustrates relative relationships between genera. These figures are only examples of the ratios, and were selected because they clearly demonstrate the results referred to below.

A multivariate analysis of variance was performed to determine the significance of differences between the four genera. The comparisons were based on a non-orthogonal set such that the differences between *Uma* and the other three genera were tested (comparison #1), the differences between *Callisaurus* and *Cophosaurus* were tested (comparison #2), and, finally, the differences between *Cophosaurus* and *Holbrookia* were tested (comparison #3).

Using 116 ratios selected in the discrimi-

nant analysis, it is possible to classify the four genera. Of 21 tests, classification agreed with the present taxonomic system in 17 of them. The first classification error was in Test 7, where a *Callisaurus* and a *Cophosaurus* were both classified as *Holbrookia*. Only three ratios were involved, and all three involved the squamosal width divided by the vomer width, palatine length, and palatine width respectively. These ratios were effective in separating *Uma* from the other three, but were not useful in distinguishing between the other three genera.

The second classification error occurred in Test 8. Here a *Callisaurus* and a *Holbrookia* were both classified as *Cophosaurus*. Four ratios were involved, and each one used the squamosal width divided by the pterygoid width, the epipterygoid width, the hyoid length, and the hyoid width. Whereas *Uma* was well separated in Test 7, it was not well separated in Test 8.

The most confused classification was in Test 15. Here one *Callisaurus* and one *Holbrookia* were both classified as *Cophosaurus*, one *Callisaurus* was classified as *Uma*, one *Cophosaurus* was classified as *Holbrookia*, and one *Holbrookia* was classified as *Callisaurus*. Two ratios were used, and they were derived from the mandible width divided by the frontal width and the nasal width. *Uma* is the most distinct in this test; however, the individual plot scores show

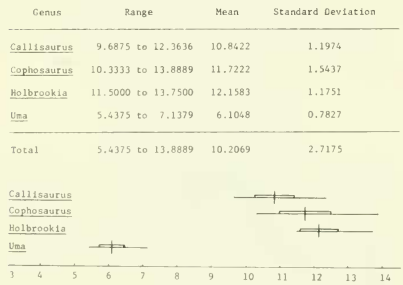


Fig. 7. Ratio of the skull length/squamosal width used in Test #5 of the Discriminant Analysis. Range, mean, and standard deviation plotted for the ratio of skull length/squamosal width in the four current genera.

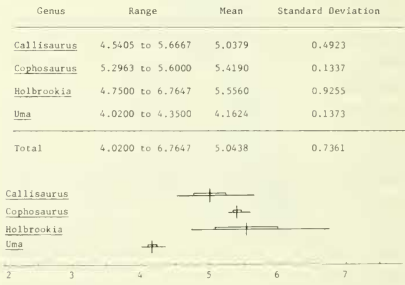


Fig. 8. Ratio of the skull length/mandible width used in Test #14 of the Discriminant Analysis. Range, mean, and standard deviation plotted for the ratio of skull length/mandible width in the four current genera.

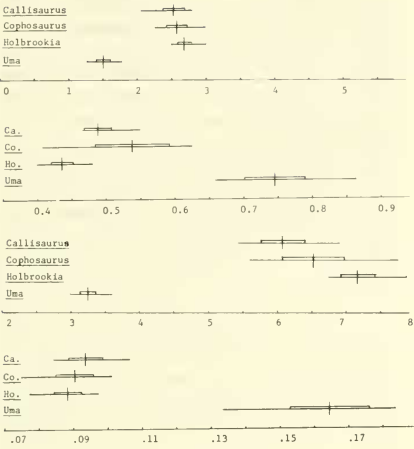


Fig. 9. Range, mean, and standard deviation in the four current genera plotted for the ratios of: A. squamosal length/squamosal width; B. squamosal width/quadrate length; C. jugal length/squamosal width; D. squamosal width/mandible length.

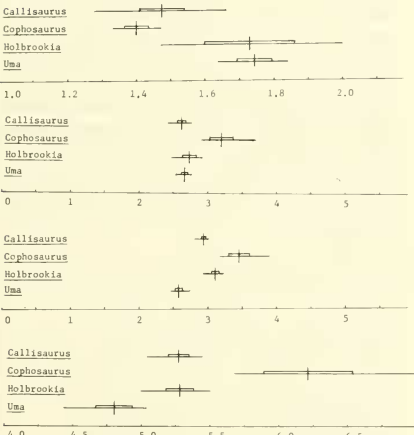


Fig. 10. Range, mean, and standard deviation in the four current genera plotted for the ratios of: A. quadrate length/quadrate width; B. squamosal length/quadrate length; C. jugal length/quadrate length; D. skull length/quadrate length.

considerable variation, and there is no discrete grouping to distinguish the separate genera.

The last confused classification was in Test 17. Here four ratios were used that involved the mandible width divided by the palatine length, palatine width, epipterygoid length, and the mandible length. In this classification a *Callisaurus* and *Cophosaurus* were both mistaken for *Holbrookia*. The plot indicates a complete separation of *Uma*, but with an overlap of the other three genera.

Over all 21 tests the centroids were separated on the average of the following distances: *Uma* was separated from *Callisaurus* by 2.10 mm, from *Cophosaurus* by 2.44 mm, and from *Holbrookia* by 2.67 mm; *Callisaurus* was separated from *Cophosaurus* by 1.19 mm and from *Holbrookia* by 1.58 mm; and *Cophosaurus* was separated from *Holbrookia* by 0.92 mm. These centroids are derived from the discriminant functions, which in turn are derived from linear combinations of the variables used in each test. The purpose for the discriminant analysis was to find ratios that would discriminate

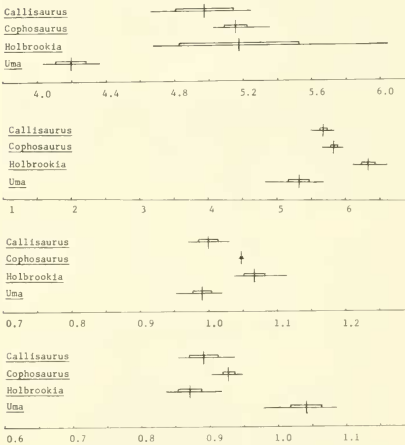


Fig. 11. Range, mean, and standard deviation in the four current genera plotted for the ratios of: A. mandible length/mandible width; B. jugal length/mandible length; C. skull length/jugal length.

between the groups; this goal was achieved. It is also desirable to determine how well each group is defined, and if it is significantly different from all other groups. The SPSS program does not provide this information, but it is possible, by studying the plots (Figs. 7-11), to see that the range of *Callisaurus* overlaps the range of *Holbrookia* and/or *Cophosaurus* in nearly all ratios plotted. The range for *Uma* is only occasionally overlapped by the other genera, and it is usually only *Callisaurus* that overlaps *Uma*.

The multivariate analysis of variance was performed to determine the degree of significance between the four genera. The non-orthogonal set of comparisons was as follows:

Comp.	<i>Cal.</i>	<i>Coph.</i>	<i>Hol.</i>	<i>Uma</i>
1	1	1	1	-3
2	-1	1	0	0
3	0	1	-1	0

The degrees of freedom, F-ratios, and actual probability for each F-value are presented in Table 1.

The differences between *Uma* and the other three genera are highly significant, but the differences between the remaining three genera are only slightly significant, and in many cases the differences are insignificant.

Uma is therefore the best differentiated by these tests. The other three genera are close together, and although they can be distinguished on the computer, their degree of separation is slight.

The probability of error in differentiating between *Callisaurus* and *Cophosaurus* is similar to the probability of error in differentiating between *Cophosaurus* and *Holbrookia* (average between 9 percent and 12 percent), verifying these statements.

These data are based on 116 ratios that were found to be the best discriminators of the 903 ratios examined. It is noteworthy that by using the very best osteological discriminators, the genera are often not clearly separated.

DISCUSSION

Sand lizards are a closely related group according to Smith (1946), Norris (1958), Axtell (1958), Etheridge (1964), and Clarke (1965). Smith referred to them as a closely knit group and listed their common characteristics as being oblique labials, granular dorsal scales, small head scales, a gular fold, a peculiar median triangular postmental, several prominent postlabials, much the same habits, similar habitat, scoop-shaped heads, flaring labial regions, and a counter-sunk lower jaw. Axtell (1958) listed 22 characters that he felt would describe ancestral sand lizards. With only a few exceptions, this list of characters might just as well apply to other sceloporine lizards.

Callisaurus, *Cophosaurus*, and *Holbrookia* exhibit many of the primitive characteristics mentioned by Axtell. Each genus, however, shows specializations that vary from those listed. *Callisaurus* is similar to Axtell's cri-

TABLE 1. Summary of F-ratios from eight multivariate analyses of variance tests.

Test df.	Comparisons		
	1	2	3
	F-ratio/Probability	F-ratio/Probability	F-ratio/Probability
1 6/7	7.797/0.79%	1.858/21.8%	4.034/4.51%
2 7/6	11.055/0.468%	4.623/4.05%	1.973/21.29%
3 7/6	25.922/0.044%	4.596/4.106%	31.230/0.026%
4 5/8	96.377/0.00062%	1.141/41.24%	2.827/9.25%
5 6/7	12.387/0.20%	16.830/0.077%	4.450/3.56%
6 5/8	40.174/0.00185%	2.100/16.76%	6.117/2.54%
7 6/7	10.251/0.35%	14.480/0.124%	2.147/17.02%
8 4/9	7.807/0.532%	4.670/2.572%	2.118/16.07%

teria for the primitive condition, with the most striking specializations being increased length of tail and limbs and a more slender body form. *Holbrookia* is also similar to ancestral sand lizards except for the covered tympanum. Body form in *Holbrookia* is not as proportionately slender as it is in *Callisaurus*, nor is the tail as long. The problematic *Cophosaurus* has characteristics of both. Its body form, limbs, and tail approach those of *Callisaurus*, but it has a covered tympanum like *Holbrookia*. *Uma* has developed, to a greater degree, the dorsoventrally flattened body and the toe fringes. *Callisaurus*, *Holbrookia*, and *Cophosaurus* occupy generalized habitats, probably similar to that of the ancestral stock. *Uma*, on the other hand, is restricted to a sand dune habitat.

Osteology

Comparisons of skulls of *Ctenosaura* (Oelrich 1956), as well as general accounts of reptile osteology by Williston (1925), Romer (1956), and Avery and Tanner (1964, 1971) indicated that osteological characteristics of iguanid lizard skulls are generally stable within a genus. Studies on *Sauromalus* (Avery and Tanner 1964), *Crotaphytus* (Robison and Tanner 1962), and *Ctenosaura* (Oelrich 1956) portrayed the apparent general stability of osteological characters found in iguanid skulls; however, skulls of *Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma* observed in this study are peculiar to iguanid skulls as portrayed by the above authors because there is stability within the sand lizard genera as a group rather than within a single genus. The lacrimals and postfrontals are also absent in all the sand lizards, a condition not generally found in iguanid skulls, except that Jenkins and Tanner (1968) found that two species groups of *phrynosoma* also lack these skull bones. Etheridge (1964) pointed out the absence of the lacrimals and postfrontals in sand lizards.

Deviation by sand lizards from the general iguanid skull, particularly evidenced by the fusion or loss of the lacrimal and postfrontal bones, is evidence supporting the hy-

pothesis that sand lizards are highly specialized among the iguanids.

In discussing the osteology of *Holbrookia*, Axtell (1958:24) stated:

In general the osteology of the genera *Callisaurus* and *Uma* corresponds closely with that of *Holbrookia*, so this discourse may apply just as well to the entire sand lizard section of the family iguanidae.

Development of the covered tympanum appears to be related to the osteological variations observed in this study. The quadrate, squamosal, paraoccipital process, and mandible are all adjacent to the ear, and all exhibit variations (Figs. 1, 2, 3, and 4). With the loss of the external ear, the quadrate is reduced in size, and the paraoccipital process is directed forward, the mandible is shortened, the squamosal is narrowed, and the hyoid is also shortened. These modifications of the skull are apparent in earless sand lizards and are less modified in sand lizards having an external ear. *Callisaurus* and *Uma* are alike in that the paraoccipital process is directed caudad, the quadrate proportionately larger, and the mandible long and wide in comparison to the earless forms (Figs. 1, 2, 3, and 4). In *Uma* the degree of development of these characters is different because the squamosal is wide. A ratio of skull length divided by squamosal width shows: (a) *Uma* ranging from 5.4375 to 7.1379; (b) *Callisaurus* ranging from 9.6975 to 12.3636; (c) *Cophosaurus* ranging from 10.3333 to 13.8889; and (d) *Holbrookia* ranging from 11.0833 to 13.7500 (from Fig. 7). The quadrate and mandible length and width are similarly enlarged in *Uma* when compared to the other groups. These differences are sufficient to permit the computer to distinguish between these measurements in *Uma* and those same characteristics found in *Callisaurus* and the earless group.

There is some variation in the position and articulation between the squamosal, jugal, and postorbital. In all except some *Uma* individuals, the jugal reaches the squamosal. In *Callisaurus* it edges between the squamosal and postorbital. In *Holbrookia* and *Cophosaurus* the degree of encroachment is increased. This may be a result of the forward direction taken by the para-

occipital process and the shortening of the jaw. *Uma* is unique in that the jugal fails to reach the squamosal in some individuals, in which case the postorbital is found wedging between them (Fig. 3). In other *Uma* individuals a mere contact is made without any overlap of the squamosal and jugal.

That these variations exist is verified by the statistical analysis. The SPSS discriminant analysis was able to identify characteristics that were capable of separating the genera into distinct groups. However, the analysis of variance points out that differences between *Callisaurus*, *Cophosaurus*, and *Holbrookia* (as identified by SPSS) are insignificant and that *Uma* is indeed a distinct group. The F-ratios derived from the analysis of variance illustrate these facts. The tests comparing *Uma* with the other three genera have high F-values (96.377 to 7.797) and consequently low probability of making classification errors (from 0.000062 percent to 0.79 percent). Therefore the differences between *Uma* and the other sand lizards are highly significant. In comparing *Callisaurus* with *Cophosaurus*, the F-values were found to be lower (16.830 to 1.141), and consequently the probability of classification error is higher (41.24 percent to 0.077 percent). Only two of the eight tests were significant (below 2.5 percent probability of error). The tests comparing *Cophosaurus* with *Holbrookia* are similar to those comparing *Callisaurus* and *Cophosaurus*. The F-ratios range from 31.231 to 1.973. The probability of error is again higher (21.29 percent to 0.026 percent). Low F-ratios and high error probability indicate that the differences between the three genera are insignificant.

Myology

The literature is void of studies dealing directly with myology of sand lizards. Earle (1961a, 1961b, 1961c, 1962) dealt with the middle ear and also touched on the myology in the ear region. In this study, we will deal only with the myology of the head and neck region. A comparison of the anterior anatomy of sand lizards shows some obser-

vable differences that are discussed below (Figs. 5 and 6).

The intermandibularis muscles show some variations that are useful in distinguishing the genera. *Uma* is most distinct, with its intermandibularis anterior superficialis muscle being fan shaped (Fig. 6). This condition is contrasted with that found in *Holbrookia*, where the transverse mandibulae muscles are so nearly parallel that the borders of each muscle are difficult to discern. *Cophosaurus* and *Callisaurus* exhibit an intermediate condition with some fanning seen, but not to the extent seen in *Uma*. *Cophosaurus* can be distinguished from *Callisaurus* in that fibers of the intermandibularis anterior superficialis extend posteromedially, and in *Cophosaurus*, a portion of the insertion of the intermandibularis anterior profundus is found anterior to the superficialis, a condition not seen in *Callisaurus*.

The depressor mandibulae also shows some variations. In the earless lizards there is an expanded anterior edge of this muscle, which partially covers the enclosed tympanum. This muscle emerges from beneath the constrictor colli to insert upon the mandible, with its most ventral fibers interdigitating at right angles with the intermandibularis posterior. Furthermore, the depressor mandibulae fibers extend much further along the mandibular ramus than in the eared genera. In *Cophosaurus* these fibers reach the mandibular ramus with only a few interdigitating with the intermandibularis posterior.

The omohyoideus is also variable in these genera. In the unfolding of the evolutionary development of the omohyoideus, a branch of the rectus cervicus originated on the scapula and inserted on the hyoid. In sand lizards it further developed into a complex of muscles. In *Uma* the omohyoideus has a second head that originates on the sternum. This then can be called sternohyoideus I. Another muscle, the sternohyoideus II, arises on the sternum, passes deep to the sternohyoideus I, and inserts on the posterodorsal edge of the ceratobranchial I. Avery and Tanner (1964) designated this muscle thyrohyoideus in *Sauromalus*, but, since it clearly originated on the sternum in

sand lizards, it is designated sternohyoideus II in this study.

A division of the omohyoideus has occurred in *Callisaurus*, *Cophosaurus*, and two specimens of *Holbrookia* (*Holbrookia lacerata* CAS 73979 and *Holbrookia m. approximans* BYU 17099). Thus, in sand lizards the muscle may have one to three origins: the most lateral dorsal one is on the scapula, the second is on the clavicle, and the most medial is on the sternum and interclavicle. The omohyoideus also has two insertions: the most lateral division inserts on the distal two-thirds of the ceratobranchial I, and the second and medial heads unite and insert on the proximal third of the ceratobranchial II and the basihyal. In *Uma* and for the most part in *Holbrookia*, such division of the omohyoideus has not occurred, and the insertion is continuous along the ceratobranchial I, the basihyal, and the proximal third of the ceratobranchial II. These myological variations, although observable, are not of great magnitude and may not be sufficient to support generic status for *Callisaurus*, *Cophosaurus*, or *Holbrookia*. In all there is an overwhelming myological similarity within these three genera, and they are obviously closely related to *Uma*.

Phylogeny

Norris (1958) and Axtell (1958) agreed that sand lizards began their radiation in early or middle Miocene. This is the time when the Sierra Madre Occidental Range of Mexico was being built by volcanism along the western and southern borders of the Mesa of Central Mexico (Schuchert 1935, Miller 1942). Axtell indicated that this volcanism split the sand lizards into two groups, a *Uma-Callisaurus* group and a *Holbrookia* prototype. Norris also believed the sand lizards were divided at this time, but indicated that *Uma* was isolated from the *Callisaurus-Holbrookia* stock. Norris further indicated that *Uma* was subsequently split by continued mountain-building processes in the mid-Pliocene, giving rise to the *exsul* group and *notata-scoparia* stocks. He also postulated that it was during this same time

that the *Callisaurus-Holbrookia* stock was divided. The data available to us from this study tend to support Norris' concepts concerning the radiation of sand lizards. According to Maslin (1952), "The basic assumption upon which all taxonomic practices rest is that similar organisms are related." If we assume that sand lizards have occupied similar habitats and have been subject to similar environments throughout their recent history, then we can assume that the degree of similarity between groups is an indication of the closeness of their relationship. Maslin (1952) also states that because internal characters are less variable, they are of much greater value in establishing relationships than are external characters. The internal characters considered here indicate a closer relationship between *Holbrookia* and *Callisaurus* than between *Uma* and *Callisaurus*, indicating that *Uma* was probably the first of the sand lizards to break away from the ancestral line.

Clarke (1965) examined the behavior and external morphology from the standpoint of 20 characters; in 14 of them *Cophosaurus* was like *Callisaurus*, in 5 of them *Cophosaurus* was unique, and in only one was *Cophosaurus* like *Holbrookia*. In discussing these comparisons he states:

The distinctness of *Cophosaurus* is evident. It is intermediate in many features between *Callisaurus* and *Holbrookia*, with the data indicating a closer affinity to *Callisaurus* than to *Holbrookia*. The uniqueness of *Cophosaurus* is most clearly shown in the distinctness of the push-up pattern.

On the basis of five characters, Clarke would separate *Cophosaurus* as a separate genus. These five characters are: (1) placement of the lateral bar: anterior for *Callisaurus*, posterior for *Cophosaurus*, and central for *Holbrookia*; (2) body shape: slender for *Callisaurus*, intermediate for *Cophosaurus*, and stout for *Holbrookia*; (3) middle ear: distinct with an external opening for *Callisaurus*, distinct without an external opening for *Holbrookia*, and intermediate without an external opening for *Cophosaurus*; (4) preferred body temperature: 39.2 C for *Callisaurus*, 38.3 C for

Cophosaurus, and 35.7–38.1 C for *Holbrookia*; and (5) push-up pattern: distinct in all three groups. In four of the five characters the differences are only comparative, and do not indicate a clear-cut distinction; only in the fifth does *Cophosaurus* show a real distinctness.

An alternate interpretation of these data would have to conclude that there is not enough difference to warrant generic status for *Cophosaurus*; indeed, there also may not be enough difference to warrant generic status for *Holbrookia*. The variations described are of the kind and magnitude used in the descriptions of species. Clarke (1965) stated that the push-up pattern is the most distinct feature of *Cophosaurus*. Carpenter (1963, 1967) described the same behavior for *Uma*, indicating that a genus is capable of supporting greater variation than Clarke has allowed for in *Callisaurus*, *Cophosaurus*, or *Holbrookia*.

Guttman (1970b) also commented on Clarke's study, stating:

A comparison of *Callisaurus*, *Cophosaurus*, and *Holbrookia* (Clarke 1965) indicated the great similarity among these genera. According to Clarke, the uniqueness of *Cophosaurus* is most clearly shown by its distinctive push-up pattern. A comparison of the display-action patterns of two species of *Urosaurus* (Carpenter 1962) or three species of *Uma* (Carpenter 1963) indicated to this writer that sufficient intrageneric variation exists to refrain from establishing a genus based on this display pattern.

Guttman was reporting his electrophoretic study of sand lizards, in which he analyzed the hemoglobin components and found that they were all identical. This is highly unusual, especially for different genera. Electrophoretic techniques have been of value in confirming taxonomic relationships. This has been demonstrated by Dessaur et al. (1962), Dessaur (1966), Gorman and Dessaur (1965), Gorman (1966), Maldonado and Ortez (1966), and Guttman (1970a and 1970b). The conclusion Guttman (1970b) came to, and the one that supports our conclusions, was that the sand lizards are more closely related than their present taxonomic status indicates.

Simpson (1945) states:

What is deplorable in splitting is the tendency to raise the ranks of groups without need, that is, without gaining any practical advantage. One of the more evident symptoms of this tendency is the appearance of many monotypic groups in classification.

The proposal resulting from this study and data examined from other studies would eliminate one monotypic genus and would provide a better indication of the close relationships that are so evident in the sand lizards.

Axtell (1958) believed that the sand lizards evolved under subhumid conditions, not greatly different than the conditions existing today in the sand lizard range. He postulates that it was during the mid-Pliocene that *Holbrookia* developed the covered tympanum. He then states, "The species previously known as *Holbrookia texana*, but which now appears to belong in the *Callisaurus* line of evolution, has probably developed the covered tympanum independently." Axtell's phylogenetic tree for the sand lizards is presented in Figure 12.

Earl (1961a, 1961b, 1961c, and 1962) indicated that *Cophosaurus* was intermediate between *Callisaurus* and *Holbrookia* in ear anatomy, but agreed with Axtell that earlessness evolved twice, reporting that re-

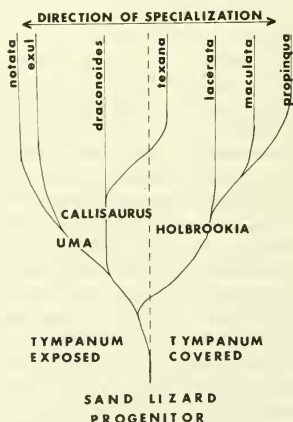


Fig. 12. Phylogeny of the sand lizards according to Axtell (1958).

lated groups have the potentiality to develop identical clines, and under similar environmental conditions these identical clines may develop at different times and places. This concept was discussed by Maslin (1952), who put forth the idea while discussing morphological criteria of phyletic relationships. Norris (1958) and Clarke (1965) also agreed with Axtell about the idea of separate earless evolution.

The concept of two evolutions for earlessness may be a major barrier to the understanding of sand lizard relationships. Since we lack a fossil record of sand lizards, there is no way of knowing when or how such a character came about. It has been suggested (Earl 1961a) that it came about in response to the burrowing habit, but this is purely speculative, as there are many burrowing species that do not have a covered tympanum (including *Uma*). A covered tympanum is not unique to "sand lizards" because the agamid genus *Tympanocryptis* in Australia is earless, and so are some of the members of *Phrynocephalus*. *Phrynosoma* has both eared and earless members. Norris's (1958) idea is acceptable when he says that *Callisaurus* and *Holbrookia* split in the early Pliocene, with *Holbrookia* occupying the table lands of the mesa of Central Mexico, and *Callisaurus* having been isolated from *Holbrookia* before their radiation to the more northern habitats. The habitats of the Chihuahuan desert and Sonoran desert are similar; the *draconoides* and *texasus* groups would have had an excellent opportunity to parallel each other sufficiently to account for the external morphologic similarities. Internal structures are not as accessible to external selective pressures and may, then, indicate more accurately the true relationships: that the *texasus* group is more closely related to *Holbrookia* than to *Callisaurus*, which it resembles through parallelism.

That earlessness may have evolved twice is possible, and it is most probable that there were separate evolutions for this character in the genera *Tympanocryptis*, *Phrynocephalus*, *Phrynosoma*, and sand lizards. To theorize that it evolved twice in the sand lizards is, however, a questionable con-

cept. Earless sand lizards are closely related, their geographic ranges overlap, their habits are similar, their food requirements are similar, the ear anatomy is similar, and we lack any evidence from fossil records that they diverged before the earless character arose. Where evidence indicates a close taxonomic relationship, as it does here, the idea of a single evolution for the earless character is most plausible. It is very unlikely that the same character would evolve twice in the same way in two groups that are as closely related as are earless sand lizards. (A proposed phylogenetic tree is given in Figure 13.)

These data, when added to that of earlier workers, seem to clearly indicate that sand lizards may best be represented by three genera: *Uma*, *Callisaurus* (as at present constituted), and *Holbrookia*.

The characteristics that separate sand lizards into genera are few and not well defined when compared to distinctions between other Sceloporine genera. The relationship between *Callisaurus* and *Holbrookia* is especially close, with earlessness (and its associated skull characters) and body proportions being the most striking variants. *Uma*, on the other hand, appears to be well defined. It is felt that *Holbrookia* is, therefore, a recent derivative of *Calli-*

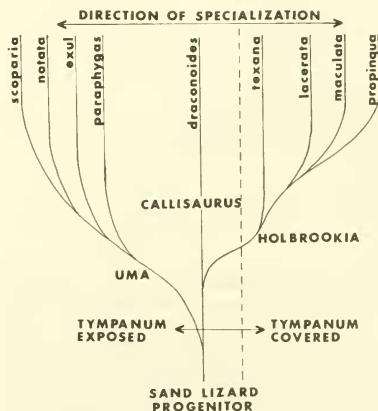


Fig. 13. Proposed phylogeny of the sand lizards as dictated by data developed from this study.

saurus, evolving earlessness and an adaptation for varied habitats in a relatively short time, perhaps since their separation in the late Pliocene.

Sand lizards, particularly the species and subspecies, particularly in *H. maculata*, indicate that this group has recently undergone adaptive radiation. If recent geological past has been correctly interpreted by recent paleontological findings (Etheridge 1961, Wells and Jorgensen 1964), the desert areas of today, extending from Texas to California, were very different as recently as 10,000 years ago, indicating that sand lizard adaptive radiation must be relatively recent.

Evidence from internal morphology and geographical distribution indicates that earless sand lizards should remain as two closely related groups in the genus *Holbrookia*. Data from comparative skull and throat anatomy, if used alone, indicate a very close relationship between all genera in the sand lizard group, but it is felt that the distinctions, however small, do indicate that *Holbrookia* has evolved from *Callisaurus* stock and has achieved sufficient distinctness to be given generic status. It is, therefore, proposed that sand lizards be classified as they were before *Cophosaurus* was split off by Clarke (1965). This is as follows:

Uma notata Baird
Uma scoparia Cope
Uma exsul Schmidt
Uma paraphygas Williams, Chraplinsky, and Smith
Callisaurus draconoides Blainville
Holbrookia texana Troschell
Holbrookia lacerata Cope
Holbrookia maculata Girard
Holbrookia propinqua Baird and Girard

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